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# Patterns in freshwater fish diversity

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## Abstract

This chapter provides a brief overview of freshwater fish diversity globally, the factors underlying diversity patterns among and within river basins and phylogenetic groups, and the main threats to this diversity in the Anthropocene. Continental freshwaters represent among the most diverse and species-dense habitats on Earth, with almost 18,000 fish species (>50% of all fish species) compressed into just <0.5% of the total surface area, and a miniscule (<0.01%) proportion of the planetary water supply. Freshwater fish diversity reaches a peak in the large lowland tropical river basins, in particular in the Amazon, Congo and Mekong basins. At an intercontinental scale, variability of freshwater fish species richness is related to the total volume and heterogeneity of aquatic habitats, and the stability of these environments over evolutionary time scales. Regional fish species richness, species composition, and functional traits all change predictably along environmental gradients from headwater to estuary (the river continuum concept). In most parts of the world, the abundance and diversity of riverine fishes is strongly related to the regular exchange of nutrients and organic matter associated with adjacent floodplains (the flood pulse concept). Freshwater fishes currently face a multitude of threats in all parts of the world, which will lead to severe losses in abundance and diversity in the absence of concerted conservation actions.

**Key words:** Biogeography, Ecology, Evolution, Flood pulse concept, Freshwater habitats, Lacustrine species flocks, Life history strategies, River continuum concept, Taxonomic and functional diversity.

## Glossary

- Allochthonous sources: externally produced, such as organic material from riparian forests
- Allopatry: originating in, or occupying, different geographical areas
- Autochthonous sources: internally produced, such as algae and aquatic plants
- Clade: a group of species that are more closely related to one another phylogenetically than to other species, which represent a single branch of the Tree of Life composed of an ancestral species and all of its descendants.
- Diversity: differences between species, or more inclusive (i.e. higher or supra-specific) taxa.
- Floodplain: area of land adjacent to a stream or river which experiences flooding during periods of high discharge.
- River capture: a geomorphological process by which the flow of a river or stream is diverted from one outlet to another.
- Species: a fundamental unit of biodiversity, biogeography, evolution and ecology. Definition of species depending on species concept (e.g. the biological species concept or the genealogical species concept).
- Speciation: the evolutionary process by which populations evolve to become distinct species
- Sympatry: occupying the same or overlapping geographic areas
- Taxon (taxa, pl): a named group of organisms in biological systematics.
- Variation: differences within a species, with trait values usually characterized by a normal frequency distribution.
- Vicariance: speciation that occurs when biological populations become geographically isolated.

## ***1. Introduction***

Freshwaters are among the most biologically diverse ecosystems on Earth, with more than 140,000 species of macroscopic fungi, plants and animals representing about 12% of all described species on earth (Reid et al. 2019). Freshwater rivers, lakes, and wetlands include about 18,000 fish species, with hundreds of new species described each year (Fricke et al. 2020). Yet all of these distinct evolutionary lineages are compressed into a habitat less than 0.5% the total continental surface area, and only about 0.3% the volume of the hydrosphere (Shiklomanov, 1998; Lundberg et al., 2000).

These myriad species exhibit a bewildering range of physiological, morphological and behavioral adaptations, which allow them to inhabit almost all continental aquatic environments. Fishes thrive in alpine lakes above 4,000 m elevation, cascades and rapids of torrential mountain rivers, benthos of deep river channels (to >100 m deep) in meandering lowland rivers, seasonally desiccated swamps and ephemeral desert pools, karstic caverns and subterranean aquifers, moist forest leaf litter, and coastal estuaries, mudflats, and mangroves swamps. Riverine fishes in particular constitute the great majority of the species and exhibit the greatest range of functional adaptations.

Freshwater ecosystems and their biodiversity are increasingly threatened by human activities, including habitat alteration, water pollution, overfishing, exotic species introduction, river diversions, fragmentation and flow regulation, expansion of agricultural and urban landscapes, rising sea levels and altered precipitation regimes (Dudgeon 2019; IPBES 2019). For freshwater fish, the rate of their decline is closely associated with the extent of riverine diversions and wetland loss (Albert et al., 2020a). Freshwater vertebrates, especially fishes and amphibians, are currently the most threatened groups of vertebrates on our planet (Reid et al. 2019).

This chapter provides a brief overview of freshwater fish diversity, summarizes the main patterns and processes in freshwater fish ecology and evolution, and highlights role of aquatic-terrestrial linkages in maintaining healthy fish populations and diversity. The last section describes the main threats to the persistence of freshwater fish diversity in the 21<sup>st</sup> Century.

## ***2. Freshwater fish***

Surprisingly, not all the fishes encountered in freshwaters are obligate freshwater species. Many freshwater fishes are **diadromous**, meaning they migrate between freshwater, defined as <500 ppm dissolved salts, and seawater to feed or reproduce. These migrations occur on time scales ranging from daily to annually or longer, and over distances ranging from a few meters to thousands of kilometers. For example, the Bull shark (*Carcharhinus leucas*) is mainly a marine species, but commonly enters freshwater rivers around the world, having been caught up the Amazon river as far as Iquitos (Peru), about 5,000 km upstream from the Atlantic Ocean. Others fish groups, like salmonids (Salmonidae) and sturgeons (Acipenseridae) are **anadromous**, hatching in freshwater but spending most of their lives feeding at sea before returning to their home rivers to spawn. Yet others fish groups



like the true eels (Anguillidae) are **catadromous**, spawning in the sea but spending much of their lives in freshwater lakes and rivers.

To distinguish among species with varying affinities to continental waters, freshwater fishes worldwide may be classified into three categories based on their physiological tolerances to saltwater (Myers, 1949). **Primary** freshwater fishes are strictly confined to freshwater, and have little or no tolerance to salty or brackish waters. As a result, marine water is an important barrier to dispersal in primary freshwater fishes. **Secondary** freshwater fishes have somewhat greater tolerance to brackish waters, but normally occur in inland continental aquatic systems rather than coastal waters or the open sea. Secondary freshwater fishes are capable of occasionally crossing narrow marine barriers. **Peripheral** freshwater fishes are members of otherwise marine groups and exhibit high salt tolerance. Such fishes are more or less permanent residents in freshwater or spent part of their life cycle in freshwater and another part in marine habitats.

These different tolerances to saltwater strongly affect fish biogeographic distributions and evolutionary histories. For example, repeated sea-level fluctuations associated with global climate (i.e. ice age) cycles during the Pliocene (c. 5.3 – 2.6 Ma) and Pleistocene (2.6 – 0.01 Ma) resulted in multiple episodes of marine transgressions and regressions, alternately inundating and exposing low-lying coastal plains and the lower reaches of rivers around the world. Rising seas result in the geographic isolation of river mouths among coastal drainages, creating vicariance events for primary freshwater fish species, while representing semipermeable filter barriers for secondary and peripheral freshwater fishes. By the same token, falling seas and receding shorelines merge the mouths of coastal rivers, allowing species to disperse (expand their geographic range) and thereby lowering their extinction risk (Leprieur et al., 2011; Abreu et al., 2020).

Differences in salt tolerance also help illuminate the origins of insular freshwater faunas. Continental islands like Trinidad or Britain, with a geological history of being connected to an adjacent landmass, usually share primary freshwater fishes with the mainland. Oceanic islands however, like Iceland or Hawaii which have never been connected to a continent, have no native primary freshwater fishes. The fish species of oceanic islands are usually secondary or peripheral species.

### ***3. Global patterns in freshwater fish diversity***

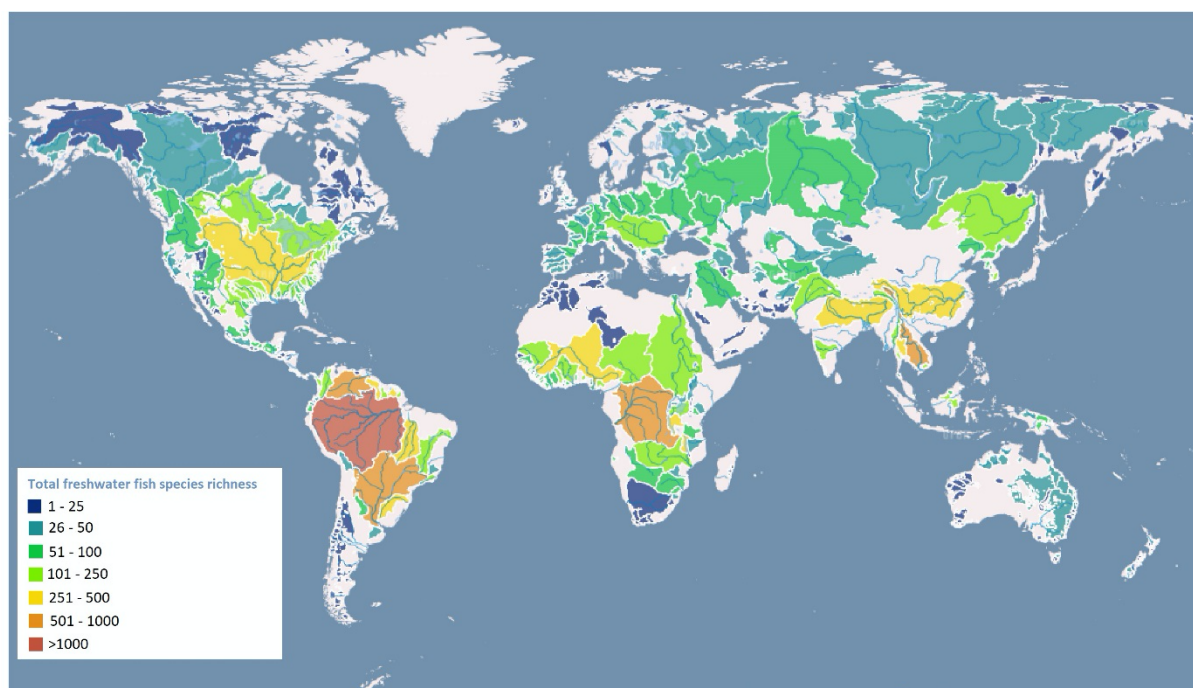
Freshwater fish diversity is highest in large tropical river and lake basins, such as the Amazon, Congo and Mekong, and large ancient lakes such as those in the Rift Valley of East Africa (Fig. 1). Islands commonly have lower freshwater fish diversity than continental areas of the same size, and a lower percentage of primary freshwater fishes. At the intercontinental scale, variability of riverine fish species richness has been related to three main factors: the total amount of aquatic habitat, spatial heterogeneity of aquatic habitats, and the stability of aquatic environments over evolutionary time

scales. These factors are all interrelated, and their relative contribution in a specific region is difficult to assess.

*Habitat volume.* The effects of river basin size and total amount of aquatic habitat is known as the species-discharge relationship (McGarvey and Terra, 2016; Rolls et al., 2018). Large river basins generally hold more species than smaller ones. All else being equal, larger drainage basins contain larger fish populations than smaller ones, which decreases the probability of an extinction after catastrophic disturbance events. Furthermore, larger river basins generally also have greater habitat diversity, and thus more potential niches that can be exploited, compared to smaller rivers.

*Habitat heterogeneity:* The number of fish species is positively correlated with measures of habitat variability and its spatial turnover (Heino, 2011; Dias et al., 2014; Craig et al., 2020). One main reason for the remarkable species richness in freshwaters is the heterogeneous distribution of freshwater habitats across biogeographic space and through evolutionary time (Albert et al., 2018). The unique geographic conditions of riverine and lacustrine environments allows fish populations many opportunities to disperse, thereby lowering their extinction risk (Miller and Román-Palacios, 2019), and to become geographically disconnected, thereby increasing the chance of speciation (Carrete Vega and Wiens, 2012, Bloom et al., 2013). By contrast, most marine environments are highly connected, and rates of lineage accumulation are generally lower in oceanic groups of organisms (Miller, 2020; Rabosky, 2020).

*Habitat persistence and biome stability:* Differences in species richness may also reflect the degree to which rivers have been recolonized since the last major climatic or tectonic disturbance event, and thus degree to which the ecosystems have reached an equilibrium level of species richness (Rabosky, 2009). Temperate and boreal rivers tend to have fewer species than tropical rivers of the same size, which can be understood in part by the more severe impacts of glacial intervals over the last 2.5 million years. Many rivers at high latitudes did not exist during the last glacial maximum (~20,000 years ago) and exhibit a relatively low diversity as they are still being colonized (Knouft and Page, 2003). By contrast, the large tropical river basins with the highest species richness have been the location of evolutionary diversification over millions of years (Oberdorff et al. 2019).



**Figure 1** | Global freshwater fish richness patterns (rivers basins as spatial units). Map from Tedesco, Jézéquel and Oberdorff (2013), Global Freshwater Fish Species Richness; accessed through the Global Freshwater Biodiversity Atlas ([atlas.freshwaterbiodiversity.eu](http://atlas.freshwaterbiodiversity.eu)) on July 2020.

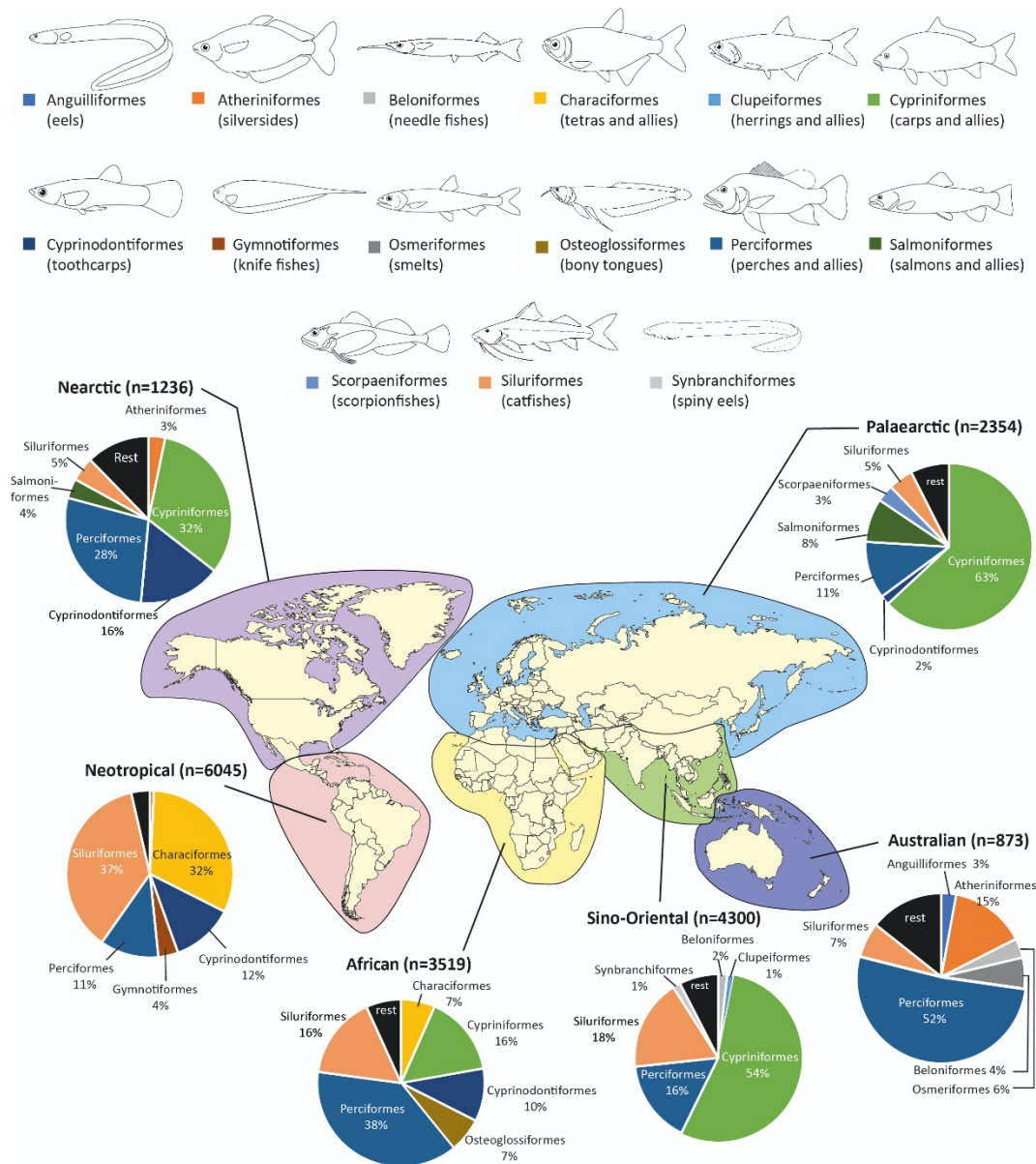
#### ***4. Freshwater fish biogeography***

##### ***4.1 Biogeographical realms***

Freshwater faunas of the world have been divided into seven main biogeographic realms based on similarities in species composition (Leroy et al., 2019). Each realm embraces a major continental landmass and is separated from the other realms by prominent dispersal barriers like oceans, mountain ranges, and deserts. The freshwater fishes realms are: (1) Nearctic, including North America and Mexico north of the Isthmus of Tehuantepec; (2) Neotropical, including southern Central America and South America; (3) Palearctic, including Europe, and southwestern, northern, and northeastern Asia; (4) African or Ethiopian; (5) Sino-Oriental, including the Indian subcontinent, China, Southeast Asia and Sundaland; (6) Australian, including Australia, New Guinea and New Zealand; and the (7) Madagascan realm. Figure 2 gives recent estimates of the freshwater fish diversity in each of these realms (Madagascar included in African realm here) and the distribution of species over the 15 fish orders that represent most of this diversity.

For freshwater fishes, each of the zoological realms may be further subdivided into freshwater ecoregions (Abell et al. 2009), whose boundaries generally, but not always, correspond with those of watersheds (i.e. drainage basins or catchments). Within an ecoregion there may be a turnover of species, such as when moving upstream or downstream within a river system (see section 4.3), but

taken as a whole, the ichthyofauna of a freshwater ecoregion has a distinct assemblage of species, although commonly overlapping with those of neighboring ecoregions. Interactive maps of these freshwater ecoregions, including descriptions of habitats and fishes, can be found on the webpage of the Freshwater Ecoregions of the World (<https://www.feow.org/>). Information and maps of the distributions of all freshwater fish families can be found in Berra (2007).



**Figure 2 | Zoogeographical realms and the taxonomic composition of freshwater fish species.** Number of species (n) in each realm and the contribution (as a percentage of the total diversity in each realm) of the six most dominant fish orders. Pie charts based on >15,000 freshwater fish species (data from fishbase.org, accessed Nov. 2019).

#### 4.2. Dominant freshwater taxa

The reasons why certain fish orders dominate in some parts of the world and are absent in others (Fig. 2) is rooted in Earth's geological history and the breakup of the supercontinent Pangea (c. 250 - 100 Ma). The distinctiveness of continental fish faunas roughly reflects the amount of time that the organisms on those landmasses have been isolated from one another. Continents that have relatively high similarity, at least at a higher taxonomic level, were connected during the more recent parts of their geological histories. The very distinct floras and faunas of the Australian realm, on the other hand, reflect their long geographic isolation from any of the other major land masses. At lower taxonomic levels, the distributional patterns of genera and species are further determined by interactions between biotic and abiotic conditions and species' functional traits (allowing them to thrive in some habitats, but not in others), as well as species' dispersal capacities (Section 5.2).

Remarkably, around 85% of the total global freshwater fish diversity belongs to just five taxonomic orders. Given their dominance, these groups are briefly described below.



Characiformes (tetras and relatives) are known from more than 2,000 species, including tetras and piranhas. All are primary freshwater species. As a group, characiforms occur in tropical freshwater in Africa, Central and South America, with one species (*Astyanax mexicanus*) extending to the Texas border. Characiformes usually have an adipose fin, well-developed teeth in their oral jaws, a scaled body, and lack barbels. Most species grow to a relatively small adult body size (<5 cm SL), but some (e.g. *Hydrocynus goliath* in Africa and *Salminus franciscanus* in South America) can reach up to 1.3 m.

Cypriniformes (carps and relatives) are known from more than 4,600 species, including goldfish, common carp, minnows and loaches. All are primary freshwater species, with the greatest diversity found in south-eastern Asia, and the group is absent from Australia and South America. Cypriniforms are characterized by a protrusible jaw in most species, having only a dorsal fin on their back (no adipose fin), and lacking teeth on the oral jaws, but possessing unique tooth plates in their throat (the pharyngeal jaws).



Cyprinodontiformes (toothcarps) are known from more than 1,400 species, including guppies, mollies, swordtails and killifishes. They are secondary freshwater species, found mostly in freshwater and coastal marine areas, especially marshes, on all continents except Australia and Antarctica. Most species are small to medium-sized fish, with small mouths, large eyes, a single dorsal fin, a rounded or truncate caudal fin, a lateral line with pores on the head and pitted scales on the body, and pectoral fins usually set low on the body. Many species are livebearers (viviparous or ovoviviparous).



Perciformes (perches and relatives) are known from more than 10,000 species, both marine and freshwater species. Freshwater species include cichlids, freshwater sunfishes (centrarchids), and perches and North American darters (percids). They are secondary freshwater species found on all continents (except Antarctica) and in all oceans. Most, but not all species have spines present in the dorsal and anal fins, thoracic pelvic fins with one spine and five rays, ctenoid scales, two dorsal fins and no adipose fin.



Siluriformes (catfishes) are known from about 4,000 species. Most catfishes are primary freshwater species, with two families of predominantly marine species. They occur on all continents except Antarctica, and are easily recognized by having up to four pairs of barbels around the mouth, lacking teeth, usually having an adipose fin, spine-like rays at the anterior dorsal and pectoral fins, and the body naked or covered by bony plates. Catfishes have an electroreceptive sense, and most species are nocturnal.

#### ***4.3 Within river patterns: from headwater to estuary***

Despite idiosyncratic differences in taxonomic composition and evolutionary history of regional ichthyofaunas, many aspects of fish assemblage structure change predictably from headwaters to river mouth, a phenomenon known as the River Continuum Concept (Vannote et al. 1980; Fig. 3). Changes in river basin geomorphology and hydrology along the course of rivers reflect processes governing current speed, sediment load and organic matter decomposition, and allochthonous versus autochthonous production (Leopold, 1994). The taxonomic composition, phenotypic characters, and community structure of freshwater fishes in all regions of the world is strongly affected by longitudinal fluvial gradients (Matthews, 2012; Lujan et al. 2013).

Headwater streams are usually narrow and, when originating below the tree line, often over-shaded by marginal vegetation. Headwater streams generally also have cooler water temperature, because of the high elevation and the rapid flow rate down steep terrains. Consequently, in-situ productivity is low and food chains relatively simple and short, depending strongly on allochthonous inputs from terrestrial photosynthesis. In headwaters that lie above the tree line the predominant fishes are small-bodied algae-grazers.

Mountain-dwelling fishes usually exhibit morphological and ecophysiological specializations that facilitate life in high-elevation and torrential waters; i.e. rheophily. Rheophilic fish species commonly possess streamlined bodies or morphological structures that allow them to cling to bottom substrate, such as fin hooks, and mounts or fins shaped to form a sucker disk (Lujan and Conway,

2105). As headwaters are usually oxygen rich water, headwater specialist fishes have low tolerance to low oxygen levels such as can be found in lower sections of river.

Mountain and hill-stream fishes have evolved multiple times independently in each of the world's major mountainous regions (Albert et al., 2018). North American groups include the rainbow trout and relatives (*Oncorhynchus* with 10 species) in the mountains of western North America, and minnows and shiners (*Cyprinella* and *Notropis* with 64 species), and North American darters (*Etheostoma* and *Percina* with 132 species) in uplands of eastern North America. South American groups include the characiforms *Creagrutus* with at least 75 species and *Parodon* with 15 species, the catfishes *Astroblepus* with at least 80 species, *Chaetostoma* with at least 48 species, and *Trichomycterus* with at least 49 mountain species, and the killifishes *Orestias* with 45 species.

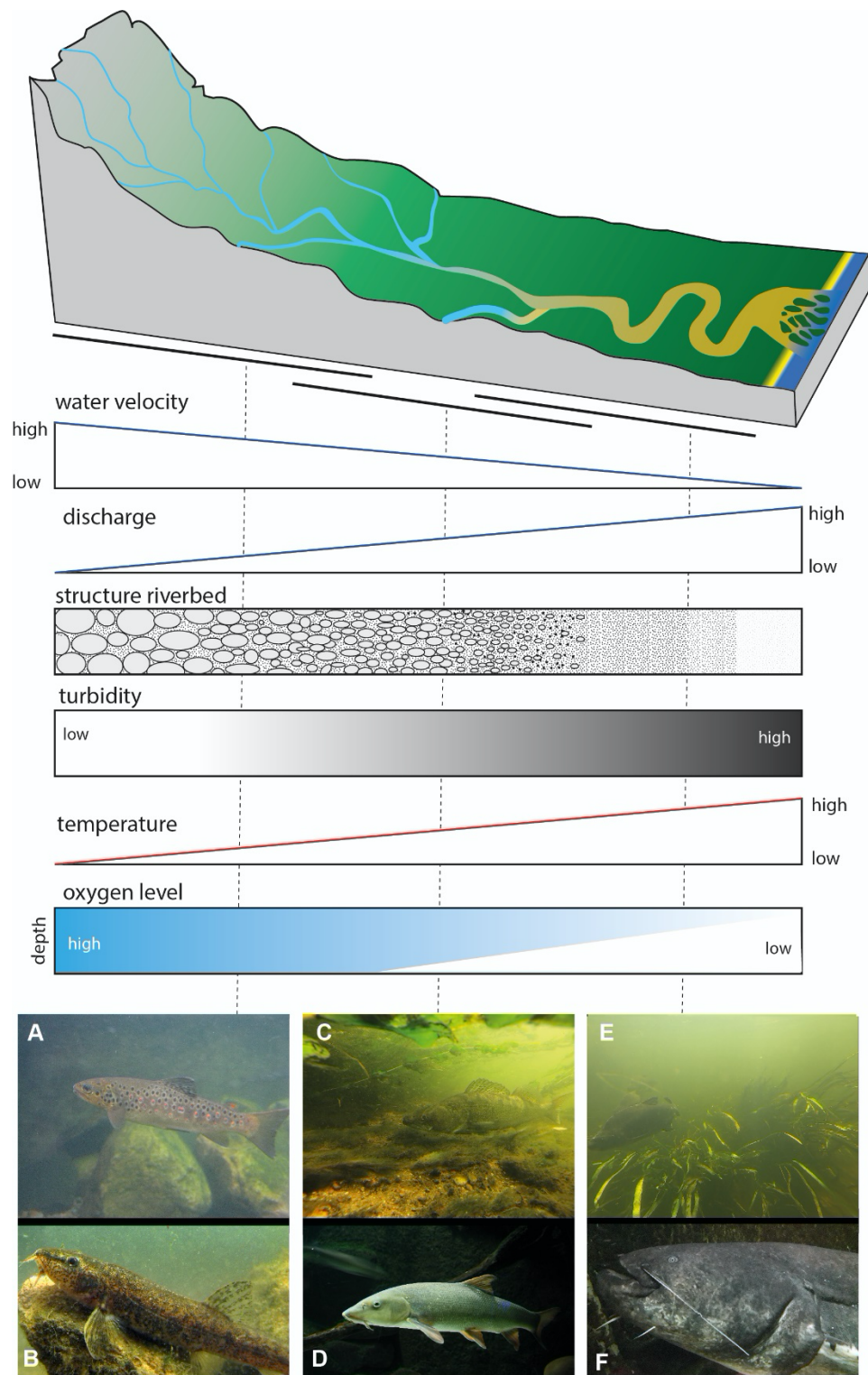
Eurasian groups include the snow minnows (Schizothoracinae) with at least 76 species in the Himalayas-Tibet region, the hillstream loaches (Balitoridae) with at least 102 species in the mountains of south and southeast Asia and Sundaland, the catfish families Akysidae with 57 known species and Sisoridae with at least 292 species. African mountain fishes include the cyprinid *Luciobarbus* with 38 species and the catfish family Amphiliidae with at least 102 species. There is also a curious group of fishes in their own family, Galaxiidae, with about 66 species that exhibit a circum-Antarctic distribution in high-altitude rivers of southern New Zealand, Australia, Africa and South America.

Middle sections have warmer water than headwaters and more autochthonous production (e.g. by algae) because of the nutrients that come down from headwater streams and because of increased light availability as rivers widen. Water flow is slower and food chains begin to lengthen. In West- and Central Europe, common fish species in middle sections are those of the genus *Barbus* (Fig. 3D), which depend on gravel beds for spawning.

Towards the mouth of the river, conditions start to resemble a slowly moving lake. Energy availability from both allochthonous and autochthonous production is high, as is energy input and dissolved organic matter from upstream reaches, leading to an increase of detritus- and plankton feeding species and mud as feeding ground. Turbidity is commonly also high and species that find food visually decrease in abundance. Oxygen levels are usually much lower compared to headwaters because of the combination of higher water temperature, lower flow rate and high decomposition of organic material. Brackish water, or occasional brackish conditions, in the lowest reaches of rivers can limit the occurrence of primary freshwater fishes, but fish diversity can be high due to the presence of secondary and peripheral freshwater fishes (see section 2).

There may be many fish species that do not clearly conform to the river continuum concept, roaming from headwater to delta, but large rivers usually have a clear turn-over of fish assemblages along their course, at least among the species that dominate.





**Figure 3** | Most rivers have a clear turn-over of fish assemblages (and dominant species) from headwaters to delta, reflecting changes in the physical environment as shown in a generalized form here. Some headwaters may originate in the lower sections of rivers (e.g. small forest creeks) and will not show pronounced changes in some of the physical properties illustrated here (e.g. temperature and structure of the riverbed). Some examples of indicator species for different river sections from the Rhine basin: (A) Brown trout (*Salmo trutta*), (B) Stone loach (*Barbatula barbatula*), (C) zander (*Sander lucioperca*), (D) common barbel (*Barbus barbus*), (E) common bream (*Abramis brama*), and (F) European catfish (*Silurus glanis*).



#### ***4.4 Importance of river floodplains for riverine fish diversity and abundance***

Although the River Continuum Concept provides an important holistic view of river systems, it initially did not consider the role that lateral floodplains play in supporting aquatic productivity. Possibly, the importance of floodplains for fish was long misunderstood because nearly all large rivers in the temperate region were already heavily modified landscapes prior to scientific study (Opperman et al. 2017). It is now broadly recognized however that floodplains play a crucial role for fish abundance and diversity, with many studies across the world showing direct relationships between fish production and the extent of floodplain inundation (e.g. Welcomme 1979; Risotto and Turner 1985; Beechie et al. 1994; Agostinho et al. 2004; Pander et al. 2015). Consequently, the river continuum concept has been extended with the flood pulse concept (Junk et al. 1989), recognizing that floodplains are intimately connected to rivers (Fig. 4).

Floodplains are inundated seasonally (predictably) in most river systems, but irregularly (unpredictable) in others. The predictably, seasonality and duration of the flooding determine the extent to which fish fauna in a river system depend on, and have developed specific adaptations for, exploiting floodplains (King et al. 2003). When flooding is predictable (e.g. annual) and duration relatively long (e.g. several months), many fish will show adaptations to exploit the abundant food resources on floodplains and will use the floodplains as spawning and nursery areas. This is the case in most large tropical rivers, such as large parts of the Amazon, Congo and Mekong. Here, the flooding season usually represents the time of plenty during which fish built up fat reserves and use floodplains for spawning and rearing (e.g. van der Sleen and Albert 2017). Predation rates are commonly low during the flooding season as fish are dispersed over large and vegetated areas. In the Amazon basin, the flooding period also coincides with the peak of the fruiting seasons of riparian trees. Many fish species feed on floodplain tree seeds and fruits, which form important nutritional items (e.g. Goulding 1980; Fig. 4). In return, fish can be important (upstream) dispersal agents of tree seeds, a process known as ichthyochory. Access to this seasonal bonanza can be limited by extreme and persistent hypoxia in tropical floodplains, caused by decomposition of forest litter during the flood season. Fishes that exploit tropical floodplains therefore commonly possess a combination of morphological, physiological and behavioral adaptation for hypoxia.

The dry season can represent the opposite case, when fishes are restricted to the main river channels or oxbow lakes on the floodplain, food availability is low, and many fish species use fat reserves, built up during the floods, to survive. Predation rates and mortality are very high during the dry season. These pronounced seasonal changes in food availability and predation risk may be an important mechanism for maintaining high levels of riverine fish diversity in tropical rivers. During the flooding season, food is abundant in such quantities that fish are not competing with each other, sharing the available resources. Any competitive advantage, and disproportional increases in population size, will be unset during the low water season, when predators likely prey on the more

abundant species, and switch to other prey species when the number of prey are reduced. As such, high predation during the low-water season may prevent any given species from becoming dominant and outcompeting others.

In temperate regions, water temperature will co-determine how much fishes can exploit floodplains. If floodplains are inundated in winter, fish may not be able to utilize the floods because of low metabolic rates and/or because of low primary productivity on the floodplains during winter. Fish in temperate region will therefore benefit most strongly from flooding in spring or summer. If that is the case, floodplains can be highly desirable habitats for juvenile fish, because of the slower water speed, usually warmer water (due to reduced flow rates), high food availability and low predation risk.

When flooding is unpredictable in timing and/or duration, such as in the Murray-Darling system in Australia, fish will lack specific adaptations for using floodplains. Nonetheless, fish still benefit from the allochthonous energy input and will use the floodplains more opportunistically. The importance of floodplain habitats for fish is difficult to overstate. Unfortunately, natural floodplains continue to be among the fastest disappearing habitats in the world.



**Figure 4** | Example of floodplain forests (flooded forests) in the Amazon basin (middle Rio Negro, Brazil), during the low-water season (**A**; October to April in this part of the basin) and high-water season (**B**, May to September). Fishes and trees; a few examples of fish utilizing floodplains at high- and low latitudes: (**C**) a small pike (*Esox lucius*) hiding in the branches of a submerged willow tree, the Netherlands. (**D**) Common carp (*Cyprinus carpio*) spawn in areas of submerged vegetation in floodplains and lakes (photo from the Meuse basin, Belgium). Carp reproduction success is restricted to years when water levels start rising in May and when high temperatures and flooding of terrestrial vegetation last for a long period during May and June. (**E**) *Brycon hilarii* and *Piaractus mesopotaminius* swimming through an open area in the middle of submerged floodplain forest, Paraguay river, Brazil. (**F**) *Brycon pesu* in a submerged floodplain forest in the lower Tapajos River, Amazon basin, Brazil. Species of *Brycon*, *Piaractus* and carps are known to disperse seeds of floodplain plants, a process known as ichthyochory.

## ***5. Taxonomic diversity of freshwater fish***

At a macroevolutionary scale, the species richness of a clade, such as a fish family or genus, is a balance between rates of speciation that increase diversity, and extinction, that reduce diversity. Rates of speciation in fishes have been hypothesized to be higher in lacustrine than riverine habitats (see section 5.2; Miller, 2020). Yet most freshwater fish diversity is thought to have arisen by allopatric speciation within the dendritic spatial geometry of continental river systems (Albert et al., 2011b; 2017; Miller, 2020). River basins have a much larger total habitat footprint than lakes, are often much older, and have a more complex history of rearrangements due to river capture and sea-level changes (Albert and Crampton, 2010; Albert et al., 2018).

### ***5.1 Taxonomic and functional disparities***

Diversity measures for freshwater fishes vary strongly among taxonomic groups. This may relate partly to the amount of research effort that has been dedicated to particular fish groups, but it is undeniable that diversity is not distributed equally across branches of the phylogeny of fishes (Alfaro et al., 2009). Among fishes, some higher taxa (e.g. families or genera) are exceptionally diverse, with hundreds of species exhibiting a wide range of functional traits, while others are represented by just one or a few species and little functional diversity. In fact, most of the higher taxa in fish, as in most groups of organisms, are species poor, while most species are members of a few species-rich groups (Albert et al., 2011a; Worm and Tittensor, 2018).

Many reasons have been proposed to explain these taxonomic and functional disparities. Some explanations focus on the role of so-called “key innovations”, novel evolutionary traits that either spur speciation or reduce extinction (Seehausen, 2006; Siqueira et al., 2020). These traits can include any aspect of an organism’s phenotype, including for example: small adult body size (Albert and Johnson, 2012), chromosomal and genomic reorganization (Volf, 2005), developmental canalization and modularity (Larouche et al. 2018), ecological specialization (Seehausen and Wagner, 2014), and specialized sexual communication systems that allow many closely-related species to co-exist together in sympatry (Crampton and Albert, 2006; Arnegard et al., 2010).

In addition, speciation rates can also relate to traits that impede dispersal, such as **philopatry** or the absence of dispersal-specialized developmental stages (Likens et al., 2009). For example, the loricariid catfishes (family Loricariidae) from South America attain relatively small adult body sizes and most species are highly territorial. As a consequence, the dispersal capacity of most loricariid species is low, which increases the chances for geographic isolation and speciation. Indeed, over 1,000 loricariid species are known. In contrast, only 114 species are known in another catfish family occurring on the same continent, the Pimelodidae, which consists of large-bodied migratory catfishes, many of which are widely distributed. Reduced dispersal capacity has been suggested as an important factor underlying species richness in many fish families.

Other explanations for differential diversification focus on properties of the external environment, including the contributing roles of ecological opportunity (Roxo et al., 2017), total amount of evolutionary time and ecological incumbency (Albert et al., 2011a), and the vagaries of random diversification (Albert et al., 2020b). Most higher taxa of freshwater fishes originated tens of millions of years ago, in the Late Cretaceous (c. 100 – 66 Ma) or Paleogene (c. 66 – 23 Ma). For example, the bowfin or choupique (*Amia calva*) of eastern temperate North America is the sole surviving lineage of the Amiiformes, a group that was once diverse and geographically widespread across much of the world during the Mesozoic period (250 - 66 Ma; Long, 1995; Arratia, 2013). Indeed, almost all of the early branches of bony fishes (Osteichthyes) are relicts of groups that were formerly diverse and widespread, and which only survive in the modern world with a few species in isolated freshwaters.

Regardless of the causes, the wide distribution of evolutionary ages among fish clades indicates that the formation of the modern biodiversity arose from interactions of landscape and biotic processes over an immense time span.

## **5.2 Lacustrine species flocks**

Some fish groups exhibit a tremendous capacity to diversify rapidly. This capacity is well-illustrated by the phenomenon of “lacustrine species flocks”, the accumulation of many closely-related species within the circumscribed area of a large lake basin (Echelle and Kornfield. 1984). Such rapid accumulations of many closely-related species, often differing from one another in traits related to feeding and habitat, have long been thought to represent classic examples of Darwin’s hypothesis for the origin of species by means of natural selection (Goldschmidt, 1998; Foote, 2018; Richards et al. 2018).

Species flocks of lake-dwelling fishes have been described on all continents except Antarctica, concentrated in regions that were previously defaunated due to climatic or tectonic events (ice ages, vulcanism), or otherwise lacking an incumbent fauna of primary freshwater fishes (Cavin, 2017). Some of the more well-studied fish lacustrine species flocks include the cottoid sculpins of Lake Baikal, Russia (with 22 spp. in two genera), *Orestias* killifishes of the Lake Titicaca basin in the Andes of Bolivia and Peru (with 23 spp.), *Coregonus* ciscos or whitefish salmonids of the Great Lakes of North America (with 8 spp.), cypriniform barbs of Lake Tana, Ethiopia (*Labeobarbus* 27 spp.) and Lake Lanao, Philippines (*Barbodes* 18 spp.), and Sailfin silversides (*Telmatherina* 10 spp.) in the Malili Lake system of Sulawesi, Indonesia.

Certainly the most spectacular of all of the fish species flocks are those of the haplochromine cichlids in the Great Lakes of the East African Rift Valley. These haplochromines have radiated into more than 3,000 distinct phenotypes, each representing a putative species lineage, in only a few millions of years or less. Lake Victoria, with a flock of 500 morphotypes, is thought to have been a dry lake-bed perhaps as little as 14,000 years ago (Meier et al., 2017). There are also at least 241

cichlids representing several different clades in Lake Tanganyika (age 9 – 12 Ma) and about 400 species representing other additional clades in Lake Malawi (age 4.5 – 8.5 Ma). There are also well-studied cichlid species flocks in smaller lakes in volcanic calderas, for example in Cameroon (West Africa) and Nicaragua (Central America).

Cichlid fishes differentiated most rapidly in aspect of their head and mouth shape, structure of the teeth in the oral and pharyngeal jaws, and color patterns based on pigment cells called chromatophores. All these tissues are derived developmentally from a unique and exceptionally plastic tissue vertebrate cell type called the neural crest (Bronner and LeDouarin, 2012; Powder and Albertson, 2016). These traits, associated primarily with feeding and sexual behaviors, allow species to occupy a wide variety of ecological roles in lacustrine ecosystems.

Species flocks have attracted much attention in the hope they would illustrate conditions in which adaptive divergence based on ecological specialization results in speciation. Yet in most cases where detailed population genetic and phylogenetic studies have been performed, the species that constitute a lake fauna have not been found to be monophyletic. Rather the species flock has been found to have accumulated through multiple rounds of dispersal and subsequent speciation, in and among the lake and tributary rivers of the regional watershed (Turgeon and Bernatchez, 2003; Lüssen et al., 2003; Martin et al., 2015). Many of the classic examples of sympatric speciation in lakes have been shown to involve complex histories of gene flow and dispersal into and out of the lake (Kontula, et al. 2003; Fruciano et al., 2016; see review by Stroud and Losos, 2016). Lacustrine species flocks in general represent cases in which both ecological and geographic factors conspired to generate rapid adaptive diversification

## **6. Threats to freshwater fish diversity**

There are hardly any large rivers systems left on our planet in which fish do not face a multitude of threats (e.g. Dudgeon et al. 2019; Reid et al. 2019). Severe and persistent pollution continues to be a major problem in many rivers and includes pesticides and fertilizers running off from agricultural land, mercury from gold mining in headwaters, microplastics, and pollutants that affect the sex ratio in fish populations. Loss, or severe reduction, of river connectivity is another major threat. The construction of large hydrological dams for power plants is a growing concern for fish diversity in many tropical rivers (Winemiller et al. 2016). Hydropower dams modify habitat conditions in large areas upriver and down-river of the dam, retain sediments and nutrients in the reservoirs, and block fish migration routes. Fish passages (i.e. fish ladders) are often insufficient to fully mitigate the loss of connectivity and obstructions to fish migration routes (Brink et al. 2018).

Dams and other water diversion structures also strongly modifying the natural flood regime downriver (Timpe and Kaplan 2017). These structures change the annual flood pulse to become highly intermittent, with important consequences for fish populations that depend on predictable access to floodplains for food, reproduction and rearing. In addition, floodplains have also been

severely modified throughout most of the world due to drainage and land-use change (e.g. deforestation for agriculture). In some parts of the world, the introduction of non-native (i.e. exotic) species is another major issue, causing (local) extinction of native species. The introduction of the Nile Perch (*Lates niloticus*) in Lake Victoria is a much studied example of the dramatic effects that alien species can have on an entire ecosystem. For other species, persistent overfishing led to the disappearance of larger individuals, with ramifications for the important ecological and demographic roles that larger individuals can play. On top of all this, climate change is becoming an increasing stress factor in many freshwater ecosystems, affecting species through warming water temperatures, shifting streamflow regimes, increasing extreme (e.g. flooding and drought) events, and facilitating species invasions.

Freshwater ecosystems and their associated riparian habitats are amongst the most biologically diverse on Earth, and have inestimable economic and cultural values. Yet human impacts to lakes, rivers, streams, wetlands and groundwater are dramatically reducing biodiversity and robbing critical natural resources and services from current and future generations. Freshwater biodiversity is declining rapidly on every continent and in every major river basin on Earth, and this degradation is occurring more rapidly than in terrestrial ecosystems (Albert et al., 2020a). Fish abundances of freshwater fish populations have become dramatically reduced since 2000, at local scales in both temperate (Freyhof and Brooks 2017) and tropical (Cohen et al. 2016a; Pelicice et al. 2017) latitudes, and in different climate zones (Ngor et al. 2018). From 1970 to 2012 populations of freshwater fishes have declined by 88%, with mega-fishes (>30 kg) undergoing the largest declines (-94%, Carrizo et al. 2017; He et al. 2019).

Many freshwater fish have narrow distributional ranges or have small population sizes, making them intrinsically rare and sensitive to local disturbances. Data suggest that up to 40% the freshwater fishes in Europe and North America are at risk or already lost (Maitland 1995; Jelks et al. 2008). Globally, it is estimated that 20% of all freshwater species have become extinct or face extinction in the decades to come, and this percentage will likely continue to increase in the future. The Yangtze basin is among the most impacted of any large river on Earth, with the recent extinction of the Yangtze paddlefish *Psephurus gladius* (Zhang et al. 2009). The Yangtze paddlefish was the last surviving species of a lineage that originated in the super-greenhouse world of the Mesozoic, with fossils from the Upper Cretaceous about 75 million years ago.

Effective management of freshwater resources and ecosystems must be ranked amongst humanity's highest priorities. The remedies - restrictions to the construction of dams, pollution control, restoration of wetlands areas, limits on harvests of vulnerable species, and restrictions on the translocation of non-native species – are well known, but modification and degradation of river systems still outpaces initiatives to mitigate the threats to freshwater diversity in most parts of the world. Freshwater faunas worldwide are imperiled and the future looks bleak for many freshwater fish



species. Coordinated actions are urgently needed at the local, regional and international levels, in order to conserve freshwater habitats and species that have taken millions of years to evolve.

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### Relevant internet sources

- Information on global freshwater fish diversity patterns: <http://atlas.freshwaterbiodiversity.eu/>
- Maps and information on the freshwater ecoregions of the world: <https://www.feow.org/>
- Global database on fish species (e.g. taxonomy, ecology, distribution):  
<https://www.fishbase.org/>
- Database and reference work on the scientific names of fish species:  
<https://www.calacademy.org/scientists/projects/eschmeyers-catalog-of-fishes>

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